STUDIES OF THE COMPOSITION OF DECIDUOUS FOREST TREE LEAVES BEFORE AND AFTER PARTIAL DECOMPOSITION[1]

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INTRODUCTION

Podsol soils have been intensively studied ever since the pioneer researches of Dokuchaev (9), yet the mechanism of their development is still obscure. It is generally assumed that acidic substances are responsible for the transport of bases during podsolization and many of the earlier investigators (9) stressed the importance of organic acids in this process. However, the only evidence supporting this idea was the presence of an acidic A_0 layer, as organic acids were not isolated from soil until 1913 (26). Uronic carboxyl groups have also been proposed as the agents involved in podsolization (19).

In view of the importance of podsol soils in Eastern Canada (29) an investigation of the fundamental processes responsible for their development was started at Macdonald College in 1947. The problem is being approached through a study of the acidic components leached by natural rainfall from decomposing leaves of deciduous forest trees. In connection with this work it was important to know the annual leaf-fall of the different species of trees and the nature and extent of decomposition of the leaves during weathering. These studies are described in the following sections of this paper.

EXPERIMENTAL PROCEDURE

Selection and Preparation of Sampling Areas

In September, 1947, sites were selected in the Morgan Arboretum at Macdonald College for the purpose of collecting and measuring the autumn leaf-fall of the following species of trees: American beech (*Fagus grandifolia* Ehrh.); gray birch (*Betula populifolia* Marsh.); sugar maple (*Acer saccharum* Marsh.) and poplar (*Populus grandidentata* Michx. and *P. tremuloides* Michx.).

The beech and maple stands are mature, quite dense and free of other species, situated on deep sand and glacial till, respectively. The birch areas were located in a relatively open pasture on a mixed sand and clay formation in 1947 and 1948. New sites were selected in 1949 under more dense growth on deep sand. In 1947, the poplar leaf-fall was a mixture of nearly one-third *P. tremuloides* and two-thirds *P. grandidentata*. The stand was thin and mixed with birch, maple and evergreens. New sites were selected in 1948 under a thin, mature stand of *P. grandidentata* located on imperfectly drained sand.

All undergrowth and loose, partly decomposed litter were removed from the selected areas which were then enclosed with rot-proofed canvas windscreens. Several sites were prepared under each species. The total area enclosed by windscreens was nearly 400 sq. ft. under beech and poplar, 500 sq. ft. under maple and 750 sq. ft. under birch.

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Collection of Leaf-litter

The leaves falling within the enclosed areas were collected at frequent intervals during the period of leaf-fall. Beech, maple and poplar leaves were picked up by hand. The birch leaves, collected with a hand-rake, were contaminated with a small amount of grass. Leaves of other species falling inside the screened areas were discarded. In 1947, eleven collections were made between October 9 and November 4 when leaf-fall was complete. Only in one or two instances were the fallen leaves exposed to rain before being collected. Collections were made from September 29 to November 11 in 1948. The weather was less favourable than during the previous season and an estimated 50 per cent of the leaf-litter was leached to some extent by rain before harvesting. In 1949, leaf collection began on October 1 and was completed on November 6. Only the last collection was severely leached before harvest.

The leaves of each species were put in separate bags as collected and stored in a small building in the arboretum. When leaf-fall was finished, each species was thoroughly mixed and weighed. Known quantities were exposed to weathering as described in the following section and the remainder taken to the laboratory for analysis.

Methods of Weathering Leaves

The leaves collected in 1947 were exposed to decomposition by rain and microorganisms under two different conditions.

A known quantity of leaves of each species was placed on 1/8-in. mesh wire screens, supported on trays specially designed to collect the natural rainfall percolating through the layer of leaves. Each tray was 4 ft. × 3 ft. × 10 in. with a bottom sloping towards the centre and front terminating in a pipe connected to a covered pail. The trays were set into the ground with the top about one inch above ground level. A trench was dug the required depth to hold the pails for collecting the leachates resulting from natural rainfall. Each tray was covered with 1/4-in. mesh wire screens to exclude small animals, wind-blown leaves, etc. All surfaces of screens, trays and pails were treated with asphalt paint to inhibit corrosion. The leaves were exposed in the trays for 11 months.

To compare the degree of decomposition of leaves in trays with that of leaves lying over soil, a known amount of each species was exposed to weathering for 10 months on 1/8-in. mesh wire screens (4 ft. × 3 ft.) in contact with the ground and held in place by canvas windscreens. These were located on a single soil type in the vicinity of the trays.

METHODS OF ANALYSIS

Analysis of Leaf Material

Samples of the freshly fallen leaves and the residues from the trays and ground-screens were air-dried in the laboratory, weighed, thoroughly mixed and a representative portion of each ground in a Wiley Mill so that all of the material would pass through a 20-mesh sieve. The chemical determinations were made on representative sub-samples of this ground material.

Moisture was calculated as the loss in weight when two-gram samples were dried to constant weight in an electric oven at 105° C.

Ash was found by igniting weighed samples in porcelain crucibles in a muffle at 600° C.

Total nitrogen was determined by the micro-Kjeldahl method (20).

Lignin determinations were made by the 72 per cent sulphuric acid method as described by Ritter and co-workers (25), after removal of extractives and pretreating with one per cent hydrochloric acid.

"Extractive-free" material for subsequent holocellulose determinations was prepared by a modification of the procedure employed for wood (30). Weighed samples of ground leaf material were transferred to fritted glass extraction thimbles (C porosity) and extracted in a Soxhlet for 16 hours with alcohol-benzene solution (32 parts by weight of alcohol and 68 parts by weight of benzene). The residue was washed several times with alcohol on a Buchner, using light suction, and allowed to air-dry until free of alcohol. It was then refluxed for three hours with distilled water (150 ml./g.), filtered, washed several times with hot water, and air-dried. Quantitative estimation of the alcohol-benzene and hot water soluble material was obtained using five-gram samples. Large batches of "extractive-free" material were prepared using 15-g. samples for the first extraction and combining the contents of two thimbles for the boiling water digestion. Any sand contaminating the leaf material remained in the digestion flask when the extracted residue was carefully transferred to a Buchner by successive washings with hot distilled water. It was collected in a tared Gooch crucible, ignited at 600° C. and weighed. The mean of six 30-g. samples was calculated as per cent sand. All results in this paper are reported on the basis of the sand-free materials.

The "extractive-free" material was used for the determination of holocellulose, employing the acid chlorite method of Wise, Murphy and D'Addieco (35).

Alpha cellulose was determined as described by Ritter (24) on samples of air-dried holocellulose.

Analysis of Leachates

The leachates were collected from the trays at each rainfall during the period of weathering except for the winter months. They were filtered to remove any suspended matter and the volumes recorded. Titratable acidity or alkalinity was determined by titrating a suitable aliquot to pH 7 with 0.01 N hydrochloric acid or sodium hydroxide; pH was measured with a potentiometer using a glass electrode. Non-volatile solids and ash were found by the methods used for potable water (20). Ash alkalinity was determined by the method described by Purves (22).

RESULTS AND DISCUSSION

The Amount of Leaf-Fall from Hardwoods

The leaf-fall of beech, birch, maple and poplar trees was measured for three successive years. The results are given in Table I.

The yield was highest from maple followed by beech, birch and poplar. The leaf-fall varies considerably from year to year, particularly under birch and poplar, indicating these two species may be more susceptible to variations in climatic conditions than maple and beech.

TABLE 1.—ANNUAL LEAF-FALL OF FOUR SPECIES OF DECIDUOUS FOREST TREES

(Values represent pounds of dry matter per acre)

Species	1947	1948	1949	Average
Maple	2690	3116	3225	3010
Beech	1689	2096	2043	1943
Birch	1136	2341	1032	1503
Poplar	1421*	2044	1002	1489

* Mixture of *P. grandidentata* and *P. tremuloides*.

Except for maple, the leaf-fall in the Morgan Arboretum appears to be less abundant than in New York State. Chandler (5) found the fall of hardwood leaf litter ranged from 2425–3020 lb. of dry matter per acre on several soil types in 1940. The average fall of litter from conifers is of the same magnitude as from hardwoods. Thus a mixed stand of white and Norway pine in southern New England gave an annual yield of 2000–3000 lb. of litter per acre (17).

According to Lutz and Chandler (11) tree leaves are the largest single source of forest soil organic matter. Watson (34) quotes Ebermayer who found the annual leaf-fall in a mature beech forest nearly equivalent to the fall of wood.

The Composition of Freshly Fallen Leaves

The mineral composition of forest litter has received considerable attention (2, 5, 6, 10, 14, 16, 28), but there is little information available regarding the organic composition of leaves of different forest trees. In Table 2 are recorded the analyses of freshly fallen leaves collected in 1947.

Maple leaves have the highest ash content of the four species. Lutz and Chandler (11) give the average ash content of maple leaves as 11.85 per cent. Of the common hardwoods, maple leaves generally have the highest ash content. Melin (15) found the ash content of beech leaves to be

TABLE 2.—THE COMPOSITION OF MATURE LEAVES FROM FOUR SPECIES OF DECIDUOUS TREES

(Values represent percentages based on dry matter)

Fraction	Beech	Birch	Maple	Poplar*
Ash	9.44	7.21	12.33	9.41
Nitrogen	0.81	1.12	0.83	0.84
Alcohol-benzene soluble	16.18	18.30	20.42	19.54
Hot water soluble	13.63	21.48	23.68	22.03
Apparent lignin, ash free	24.03	21.87	15.49	20.00
Holocellulose	35.15	24.89	26.82	27.09
Alpha cellulose			18.06	18.91
Hemicellulose, crude			8.76	8.18

* Mixture of *P. grandidentata* and *P. tremuloides*.

9.36 per cent although the average of several reported values is 7.37 per cent (11). Leaves of *P. grandidentata* and *P. populifolia* had ash contents of 3.85 and 4.07 per cent, respectively (15). Numerous investigations have shown that the ash content of forest tree leaves may vary considerably according to species, age of the leaves and composition of the soil.

The nitrogen contents of the leaves as found in the present study are in general agreement with those reported in the literature (11, 5, 10).

Melin (15) determined the proximate composition of several species of mature freshly fallen leaves using Waksman's modified method (31, III). Three of the species, beech, maple and poplar were used in the present study and although different analytical methods were employed it is of interest to compare the results. Reasonably good agreement was obtained for the carbohydrate and lignin fractions, except for the lignin content of poplar leaves. Melin (15) reports a value of 32.69 per cent as compared to 20.00 per cent found in the present study. A higher content of water soluble material and substances soluble in organic solvents was found in the present work as compared to those found by Melin, except for the water soluble content of maple leaves which agrees fairly well. The differences in the analyses may be partly due to the fact that the leaves analysed by Melin were not representative of the total leaf-fall. In both studies, the species appear in the same order with regard to content of "extractives", i.e., maple, poplar and beech.

Decomposition of Freshly Fallen Leaves

Visual observations during the summer of 1948 indicated that maple and birch leaves decomposed more rapidly than those of poplar and beech. These observations are confirmed by the data given in Table 3 for leaves collected in the autum of 1947.

Birch and maple leaves decomposed nearly the same amount on the trays and over the soil. Beech and poplar leaves weathered more extensively in contact with the soil than in the trays.

The above experiment was repeated using leaf-litter collected during the autumn of 1948 and exposing an amount of each species equivalent to 10 times the fresh weight collected per 12 sq. ft. of ground surface. The

Table 3.—Loss in weight of leaves exposed to weathering in trays and in contact with the soil.

(Basis: 100 g. oven-dry unweathered leaves)

Species	Trays*		Soil*	
	Original weight (g)	Loss (%)	Original weight (g)	Loss (%)
Beech	3218	18.2	7012	30.3
Birch	6022	38.2	8184	41.6
Maple	3581	42.7	7209	41.0
Poplar†	2996	24.5	5519	35.1

* After 11 months on trays and 10 months over soil, respectively.
† Mixture of *P. grandidentata and P. tremuloides.*

amounts exposed in the trays and in contact with the soil ranged from 2560 g. of poplar to 3899 g. of maple leaves. Under these conditions decomposition in every case was considerably greater in the trays than over soil, although less than the previous year. In both experiments the loss in weight was nearly the same for maple and birch, less for poplar, and beech leaves were most resistant to decomposition.

It was noted that the leaves exposed in the trays and on the ground in 1949 dried out more rapidly following a rain than in 1948, presumably because of the larger quantity of leaves on the screens in 1948. Also, the tray residues contained more moisture than the ground residues when sampled in September, 1949, the soil apparently acting like a blotter. The total precipitation from April to September at Macdonald College was four inches higher in 1949 than in the previous year; however all of this excess fell in April and September. Precipitation during the summer months was very nearly the same in both years. Bartholomew and Norman (3), and Waksman and Purvis (33) have emphasized the importance of moisture in the microbiological decomposition of organic materials. In the present study, it appears that the rate of decomposition is markedly influenced by the moisture content which in turn is affected by the quantity of material, the conditions of exposure and climatic conditions.

It is interesting to compare these results with those obtained by other workers. Lunt (10) obtained losses of 2.7 and 7.0 per cent respectively, on exposing mature beech and maple leaves to natural weathering for seven weeks. Gustafson (8) found that freshly fallen maple leaves lost 30 per cent of their dry matter during exposure on the ground in a mixed stand of hardwoods for one year. Melin (15), and Broadfoot and Pierre (4) studied the decomposition of various species of forest leaves under controlled conditions in the laboratory. Beech leaves were most resistant to decomposition, birch was readily attacked, while maple and poplar were intermediate. The agreement between the results of these investigators and those obtained in the present study is significant, particularly when it is considered that the conditions were quite different in the various investigations.

Changes in the Composition of Leaves during Weathering

The decomposition of plant materials is influenced by many factors, such as the nature of the fresh material, the environmental conditions and the microorganisms and fauna concerned. Many investigators (12, 13, 15, 18, 23, 31, 34), have shown that there is a rapid loss of water soluble substances such as sugars, starches, and nitrogenous compounds in the initial stages of decomposition. The components of the cell wall are attacked less rapidly. Cellulose may disappear completely after a period of time, but lignin is relatively resistant to microbiological attack.

The general group of hemicelluloses appear to be attacked fairly rapidly, particularly in the early stages of decomposition. However, it must be emphasized that these conclusions are based mainly on results obtained by the proximate analysis of plant materials and soil. This method of study does not distinguish between living and dead organic matter or between plant remains and organic matter of microbial origin. Over 30 per cent of the organic matter in fertile soils may be microorganic, consisting of nitrogenous compounds, humus-like substances and complex carbohydrates (7). Thus it is evident that the method of proximate analysis provides a very incomplete picture of the changes which take place in decomposing organic matter.

The composition of the partially decomposed tray residues, resulting from the weathering of leaves collected in 1947, is given in Table 4. Changes in composition, calculated as percentages of the amounts of the different fractions present in 100 g. of oven-dry original leaves (see Table 2), are recorded in Table 5.

The greatest losses have occurred in the alcohol-benzene soluble, hot water soluble, ash and holocellulose fractions of all species. The decrease in the holocellulose fraction of poplar appears to be due almost entirely to loss of alpha cellulose. The crude hemicellulose (holocellulose-alpha cellulose) content of partially decomposed poplar leaves is only slightly less than in the unweathered leaves (see Tables 2 and 4). The loss of hemicelluloses was probably more extensive than indicated by the data since the yield of holocellulose was always less than the theoretical quantity, pre-

TABLE 4.—THE COMPOSITION OF LEAVES COLLECTED IN 1947 AFTER ELEVEN MONTHS WEATHERING IN TRAYS

(Basis: 100 g. of oven-dry unweathered leaves)

Fraction	Beech	Birch	Maple	Poplar
Ash	7.50	3.47	5.52	6.72
Nitrogen	0.92	1.18	0.69	0.79
Alcohol-benzene soluble	7.00	6.91	5.82	8.95
Hot water soluble	7.33	6.16	10.41	7.12
Apparent lignin, ash free	25.72	24.32	13.57	27.92
Holocellulose	28.58	12.44	15.40	17.46
Alpha cellulose	—	—	8.95	9.38
Hemicellulose, crude	—	—	6.45	0.08

TABLE 5.—PERCENTAGE CHANGE IN THE COMPOSITION OF LEAVES DURING WEATHERING

(Basis: 100 g. of oven-dry unweathered leaves)

Fraction	Beech	Birch	Maple	Poplar
Ash	−20.5	−51.8	−55.2	−28.5
Nitrogen	+12.3	+ 5.3	−16.8	− 5.9
Alcohol-benzene soluble	−56.7	−62.2	−71.4	−54.1
Hot water soluble	−46.2	−71.3	−56.1	−67.6
Apparent lignin, ash free	+ 7.1	+10.1	−12.3	+39.6
Holocellulose	−18.6	−50.0	−42.5	−35.5
Alpha cellulose	—	—	−50.4	−50.3
Hemicellulose, crude	—	—	−26.3	− 1.2

sumably due to hydrolysis of some of the hemicelluloses during acid chlorite digestion. Adams and Castagne (1) obtained evidence of hydrolysis of hemicelluloses when preparing holocellulose samples of cereal straws. Similar results were experienced in the preparation of wood holocellulose (36). The theoretical holocellulose content of a plant material is obtained by subtracting from 100, the sum of the percentages of ash, lignin and protein (N × 6.25) in the oven-dry extractive-free material. The percentage holocellulose in the unextracted original tissue may then be calculated using a factor determined by the analytical results.

The increase in the apparent lignin content of poplar leaves, and to a less extent in birch and beech, as a result of decomposition emphasizes the inadequacy of the method of determining lignin. Waksman (32) cites several papers which suggest that lignin is decomposed to some extent by certain microorganisms. On the other hand there is evidence that certain dark-colored filamentous fungi, commonly inhabiting soil and decaying plant material, may contain substances insoluble in 72 per cent sulphuric acid (21). The actual structure of lignin is unknown and as pointed out by Norman (19), there may be many lignins just as there are many proteins. Thus, it is quite evident that insolubility in 72 per cent sulphuric acid is a very empirical measure of lignin, especially in a complex system such as decomposing organic matter.

The composition of a plant material is one of several factors which influence the rate of decomposition. In general, a low content of water soluble substances and nitrogen, accompanied by a relatively high amount of lignin is conducive to slow decomposition (31, 32). Thus the slow rate of decomposition of beech leaves as compared to that of maple would be expected on the basis of their composition (see Table 2). Birch leaves contained more nitrogen than poplar which likely influenced the rate of decomposition of the former.

Characteristics of Leachates

The characteristics of the natural rainwater leachates obtained from the trays during eleven months' exposure of leaves collected in the autumn of 1947 are summarized in Table 6.

TABLE 6.—CHARACTERISTICS OF LEACHATES FROM LEAVES DECOMPOSING ON TRAYS DURING 1947–48

(Basis: Total volume of leachates collected)

Analysis	Beech	Birch	Maple	Poplar
Non-volatile solids (g.)	66.0	257.4	204.5	118.1
Ash (g.)	27.7	85.9	41.5	32.4
Titratable acidity (m.e.)	53.5	−24.7	261.7	50.8
Ash alkalinity (m.e.)	150.4	927.9	493.7	318.8
Total acidity (m.e.)	203.9	903.2	755.4	369.6
Ash alkalinity/ash	5	11	12	10

The amount of non-volatile solids and ash removed by leaching was greatest from birch, followed by maple, poplar and beech. The degree of decomposition based on loss in weight followed nearly the same order of species (see Table 3). Maple leachates had the highest titratable acidity, followed in descending order by beech, poplar and birch. Assuming that the bases were neutralizing acids, the total acidity was calculated by adding together the values for titratable acidity and ash alkalinity. Birch and maple leachates have high total acidities compared to those of poplar and beech.

The leachates of each species became progressively more alkaline with time. This is in agreement with the findings of Stepanov (27). Maple leachate was consistently the most acidic, with a minimum pH of 4.4 and a maximum of 6.5. Birch leachates collected in the late fall and early spring were acidic, but the pH increased to 7.0 by May 1 and remained alkaline throughout the season, reaching a maximum value of 7.7. Beech and poplar leachates had pH values between 5.5 and 5.8 in the fall, increasing during the following summer to neutrality or slight alkalinity. Poplar leachates were slightly less acidic than beech in most cases.

The above results were confirmed by the analysis of leachates obtained during 1948–49, from trays containing leaves collected in the fall of 1948 (see p. 460). The results appear in Table 7.

TABLE 7.—CHARACTERISTICS OF LEACHATES FROM LEAVES DECOMPOSING ON TRAYS DURING 1948–49

(Basis: total volume of leachates collected)

Analysis	Beech	Birch	Maple	Poplar
Non-volatile solids (g.)	48.6	87.0	270.6	82.6
Ash (g.)	16.8	22.7	65.4	29.2
Titratable acidity (m.e.)	21.6	−7.9	261.5	−15.4
Ash alkalinity (m.e.)	114.9	290.0	632.3	302.0
Total acidity (m.e.)	136.5	282.1	893.8	286.6
Ash alkalinity/ash	6	13	10	10

There are some differences apparently due to the amount of leaves exposed to weathering. The low content of solids in the birch leachates is surprising, particularly as the degree of decomposition of birch and maple leaves was nearly the same, 27.5 and 27.2 per cent respectively. The value obtained for alkalinity of ash may vary as a result of several factors, such as the ratio of monovalent to divalent cations and the proportion of basic to acidic oxides in the ash. However, the relative constancy of the ratio of ash alkalinity to ash for all species in both experiments suggests little change in the composition of the ash of the leaves in the two successive years. Further, the ash composition of birch, maple and poplar leachates may be essentially the same.

SUMMARY

The leaf-fall of four species of deciduous forest trees was determined for three successive years. The average yearly leaf-fall of each species in pounds of dry matter per acre was as follows: maple—3010; beech—1943; birch—1503; poplar—1489.

The proximate composition of the freshly fallen leaves of each species was determined. Maple leaves had the highest content of ash and extractives, and the lowest lignin content. Beech leaves had the lowest content of extractives and the largest amount of lignin. Birch and poplar leaves were intermediate. The holocellulose content was highest in beech leaves, followed by poplar, maple and birch.

Maple and birch leaves decomposed at twice the rate of beech leaves when exposed to weathering in trays. The differences were not so marked in the case of leaves lying in contact with the soil. Poplar leaves decomposed at an intermediate rate.

The rate of decomposition was related to leaf composition, particularly in the case of beech and maple leaves. The extent of decomposition under the conditions employed was markedly influenced by the moisture content of the decomposing material.

Ash, extractives, and alpha cellulose were quite readily removed during decomposition. Lignin and hemicelluloses were relatively resistant to decomposition. Considerable variation existed between species.

Natural rainwater leachates from maple leaves were strongly acidic throughout the season as shown by pH and titratable acidity. Leachates of birch leaves were the least acidic, while beech and poplar leachates were intermediate. In all cases the leachates became progressively more alkaline as the time and extent of decomposition increased.

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